

PATHOLOGY IN *MAJUNGASAUROS CRENATISSIMUS* (THEROPODA: ABELISAURIDAE) FROM THE LATE CRETACEOUS OF MADAGASCAR

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ABSTRACT—Recent collecting efforts (1993 to present) in the Upper Cretaceous (Maastrichtian) Maevarano Formation of northwestern Madagascar have yielded numerous specimens of the medium-sized abelisauroid theropod *Majungasaurus crenatissimus* (Depéret, 1896) Lavocat, 1955. Exquisite preservation, coupled with near-complete articulated or associated skeletons, has allowed an assessment of individual skeletal variation in this taxon, including a preliminary analysis of osteopathology in a non-tetanuran theropod. Importantly, *Majungasaurus* is the first abelisauroid theropod for which comprehensive pathology data are available. In a survey of 181 postcranial skeletal elements from a minimum of 21 individuals, abnormalities were identified in eight elements from a minimum of four individuals. These include a pedal phalanx with a mediolateral diaphyseal expansion of unknown etiology, a dorsal vertebra with a small exostosis, a caudal vertebra with probable idiopathic ossification of vertebral ligaments, and a pathologically truncated series of distal caudal vertebrae. The latter occurrence represents the first identified caudal truncation in a predatory dinosaur and only the second documented occurrence among non-avian dinosaurs.

MALAGASY ABSTRACT (FAMINTINANA)—Ireo ezaka fikarohana natao vao tsy ela (1993–hatramin'izao) tao amin'ny Cretaceous Ambony (Maastrichtian) Fiforonana Maevarano amin'ny faritr'avaratr'andrefan'i Madagasikara dia nahitana karazan-taolana maron'ny abelisauroid theropod manana vatana salasantsalany dia ny *Majungasaurus crenatissimus* (Depéret, 1896) Lavocat, 1955. Ireo vokam-pikarohana hita avy amin'ny tahiry tsara sy kanto, niaraka tamin'ny taolana mbola mifanohy na taolam-batana mbola mifangaro, dia nahafahana namantatra ny fahasamihafana teo amin'ny taolam-batan'ny tsirairay tao anatin'ity sokajy ity, ary anisan'izany ny fanadihadiana mbola santatra momba ny foforonan'ireo aretina mahazo ny taolana teo amin'ny theropod tsy “tetanuran”. Tena zava-dehibe ihany koa ny nahalalana fa ny *Majungasaurus* no theropod abelisauroid voalohany nahazoana namantatra ny rakim-pikarohana momba ny fisian'ny aretin-taolana. Tamin'ny fandinihina natao tamin'ireo karazan-taolam-batana tsy niaraka tamin'ny karan-doha ka nijerena izany tamin'ireo isam-batana 21 farafahakely, dia nahitana toetra hafa nohon'ny an'ny maro tamin'ireo singan-taolana valo tamin'ny isam-batana efatra farahakeliny. Tao anatin'izany fiavahana hafahafa izany dia nahitana fitambaran'ny taolan'ny fela-tongotra iray izay hisian'ny fivelarana eo afovoany mahazo ny sisiny, izay tsy mbola fantatra ny mahatonga ilay aretina, sy taolan-damosina iray misy fivontosana kely, ary taolan'ny rambo iray izay inoana fa nisy aretina nahatonga fahamafisan'ny hozatry ny hazon-damosina, ary karazana fiforonan'aretina nahatonga fahafohezan'ny taolan-drambo maromaro. Ity farany ity no nahitana sy nahafantarana voalohany ny aretina niseho tamin'ny taolan-drambon'ny dinaozoro mpihaza iray ary koa hany rakim-pikarohana fanindroany momba io tranga iray io tamin'ireo dinaozoro tsy “avian”.

INTRODUCTION

Paleopathology, the study of disease and other abnormalities in organisms within a paleontological or archaeological context, has played a major role in reconstructions of theropod dinosaur biology (e.g., Tanke and Currie, 1998; Rothschild et al., 2001; Hanna, 2002; Brochu, 2003). Patterns of injuries have been used to infer both interactions between conspecifics (e.g., Tanke and Currie, 1998) and predator-prey interactions (e.g., Rothschild et al., 2001; Carpenter et al., 2005). Beyond reconstructions of behavior, paleopathological information provides a glimpse into the variety of maladies that afflicted extinct species.

This study examines occurrences of pathology in a large sample of specimens attributable to a single theropod dinosaur, *Majungasaurus crenatissimus*. For two reasons, *Majungasaurus* offers an important case study for documenting pathology. First,

pathology in abelisauroid theropods has not previously been described in the literature (although Coria et al. [2002:fig. 2] illustrated but did not describe fusion between vertebral centra of caudals 5 and 6 for *Aucasaurus garridoi*). Most other studies and case reports have focused on large tetanuran theropods such as *Tyrannosaurus* and *Allosaurus* (Molnar, 2001; Tanke and Rothschild, 2002; Rothschild and Tanke, 2005). Because no comprehensive review of pathology has been presented for an abelisauroid, the use of pathology to evaluate differences in behavior or disease susceptibility across theropod clades is limited. Second, the fossil material of *Majungasaurus* is well-preserved, collected from a limited geographic and stratigraphic range in the Maevarano Formation of northwestern Madagascar, and represents the only large theropod taxon in that area. For this reason, isolated elements can be confidently referred to *Majungasaurus*, thereby maximizing the comparative sample size.

Institutional Abbreviations—FMNH, Field Museum of Natural History, Chicago, Illinois, USA; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UA, Université d'Antananarivo, Antananarivo, Madagascar.

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DESCRIPTION AND COMPARISONS

Four instances of skeletal abnormality, affecting eight elements from a minimum of four individuals, were identified in the sample (Fig. 1). These abnormalities occur primarily in verte-

brae, with one instance in a pedal phalanx. Healed fractures were also identified on ribs of a currently unprepared skeleton (Locality MAD05-42) while the specimen was being excavated in the field. No anomalies have thus far been identified in the extensive cranial remains known of *Majungasaurus*. Moreover, no anoma-

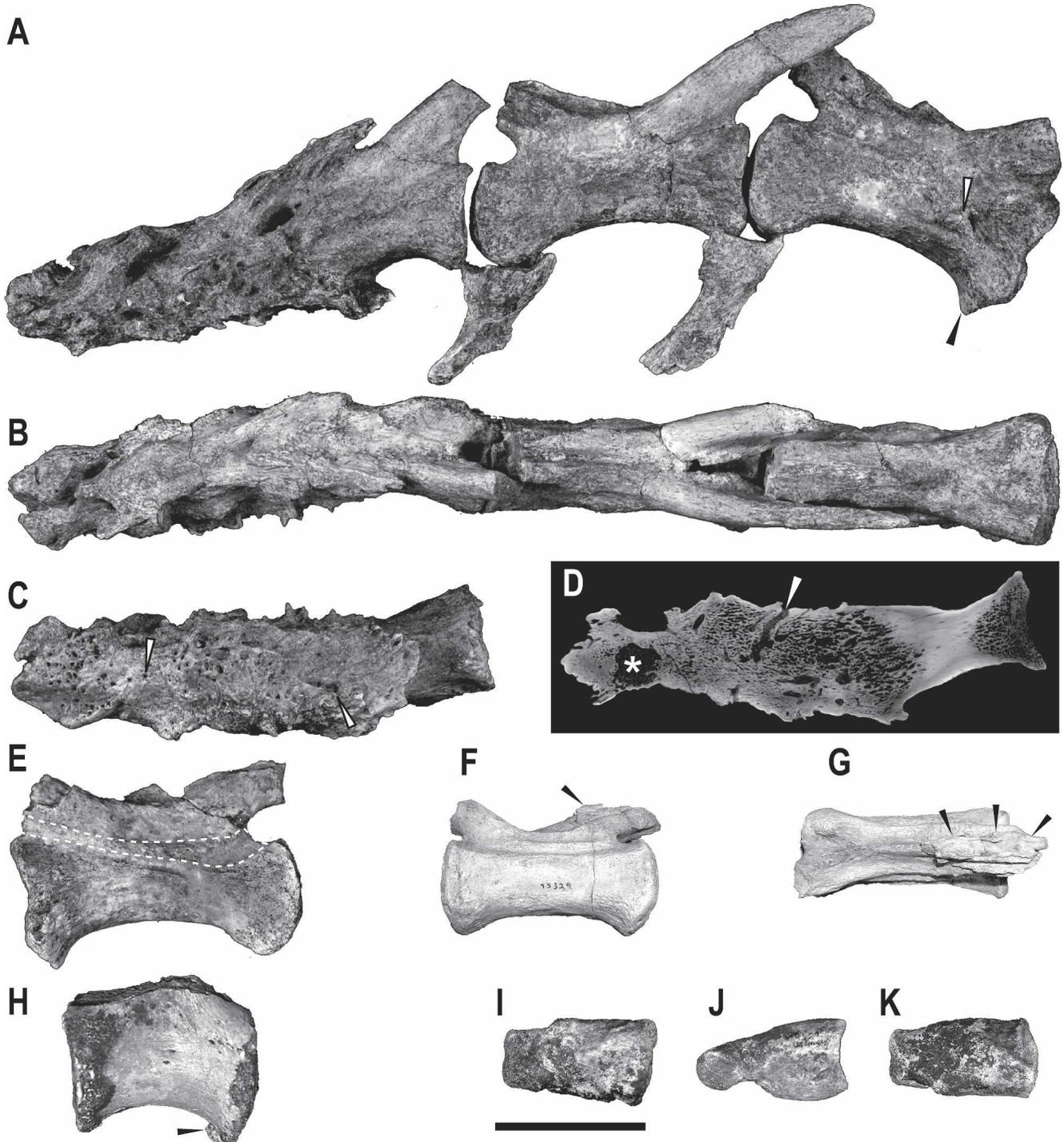


FIGURE 1. Abnormal skeletal elements of *Majungasaurus crenatissimus*. **A, B**, distal caudal vertebral series (FMNH PR 2294) in right lateral (**A**) and dorsal (**B**) views, with arrows indicating position of exostosis near cranial chevron facet and linear exostosis on lateral surface of centrum in **A**; **C**, fused distal caudal unit from same specimen in ventral view, with arrows indicating examples of cloacae; **D**, micro-computed tomography transverse slice through **C** (with cranial end to right of figure) illustrating internal cavity (asterisk) and drainage canal (arrow) within terminal mass; **E**, proximal caudal vertebra from **A** in left lateral view, with dashed lines indicating prominent neurovascular sulcus; **F–G**, caudal vertebra (FMNH PR 2442) in left lateral (**F**) and dorsal (**G**) views, with arrows indicating abnormal region; **H**, dorsal vertebral centrum (FMNH PR 2440) in left lateral view, with arrow indicating position of exostosis; **I–K**, left pedal phalanx III-1 or III-2 (UA 9058) in ventral (**I**), lateral (**J**), and dorsal (**K**) views. Scale bar equals 5 cm.

lies have been identified in samples of in-situ dentition or in the hundreds of isolated shed teeth.

Described Material

A total of 181 postcranial skeletal elements from *Majungasaurus* were examined for abnormalities, and a high-resolution cast of the skull FMNH PR 2100 was also examined. The minimum number of individuals (MNI) in the sample (21) was determined by counting the number of separate sites from which the specimens were recovered and the number of overlapping elements within these sites. Elements studied included cervical vertebrae (n = 13, MNI = 4), dorsal vertebrae (n = 15, MNI = 3), a sacrum (n = 1, MNI = 1), caudal vertebrae (n = 47, MNI = 8), cervical ribs (n = 13, MNI = 1), dorsal ribs (n = 19, MNI = 3), chevrons (n = 20, MNI = 3), a scapula (n = 1, MNI = 1), humeri (n = 2, MNI = 2), a femur (n = 1, MNI = 1), tibiae (n = 4, MNI = 4), fibulae (n = 3, MNI = 3), astragali (n = 6, MNI = 4), metatarsals (n = 6, MNI = 2), pedal phalanges (n = 27, MNI = 11), and pedal unguals (n = 3, MNI = 3). Abnormalities were evaluated by comparison with similar elements from both *Majungasaurus* and other theropods.

Vertebral Abnormalities

FMNH PR 2440—This specimen, from Locality MAD96-14, represents an isolated dorsal vertebral centrum from a subadult individual, the latter characteristic inferred from the presence of incompletely fused sutures between the centrum and neural arch. This specimen displays a small exostosis on the caudovertral surface adjacent to the cartilaginous endplate, projecting ventrally from the main body of the element (Fig. 1H). The exostosis is sharply demarcated from the surrounding bone, with a smooth external surface and somewhat ‘lumpy’ profile. In ventral view, the exostosis is V-shaped and directed cranially; it is 8 mm in length by 8 mm in width, and projects ~3 mm from the ventral surface of the vertebra. The ontogenetic stage (subadult) of the individual combined with the location and morphology of the abnormality suggests that it formed as a benign exostosis, likely of developmental endochondral origin, although ossification of a ligament or muscle attachment site (enthesopathy) is also a possibility. A marginal capsular osteophyte is unlikely, because the exostosis is located away from the presumed margins of the joint capsule. A systemic condition such as hypervitaminosis A can also be excluded, because of the restricted distribution of the abnormality on the surface of the vertebra (Lynch et al., 2002). A benign neoplasm (e.g., osteoma or osteochondroma) is also possible, but is typically rare in the vertebral column, at least in humans (Aufderheide and Rodriguez-Martín, 1998). As such, the cause of this abnormality cannot be precisely determined at present.

FMNH PR 2442—FMNH PR 2442 is a distal caudal vertebra recovered from Locality MAD93-18 that displays an abnormal growth on the dorsal aspect of the neural spine (Fig. 1F, G). The abnormality is manifested as an asymmetric, mediolaterally expanded bony growth with parallel craniocaudally trending grooves extending for approximately 3 cm on its surface. The ossification may have been more extensive in life, with portions broken off postmortem. The condition compares closely with morphology on a distal caudal vertebra of *Masiakasaurus knopfleri* (FMNH PR 2110). Most likely, these instances represent idiopathic ossification of the interspinous or supraspinous ligament. An enthesophyte at the insertion of the ligament (perhaps due to mechanical strain) is another possibility. A similar condition was reported in *Allosaurus* (Hanna, 2002). FMNH PR 2442 was collected from a quarry that contained other, non-pathological *Majungasaurus* elements, including two caudal vertebrae, a humerus, five pedal phalanges, and one pedal ungual.

An associated series of pathological caudals (FMNH PR 2294, described below) was also recovered from the same quarry. However, the much smaller size of FMNH PR 2442 relative to the most proximal vertebra in the truncated series FMNH PR 2294 strongly suggests that the two specimens are from separate individuals. Thus, these specimens are regarded here as distinct specimens. The disarticulated nature of the rest of the material in the quarry precludes definitive assignment to a particular individual.

FMNH PR 2294—This specimen, collected from Locality MAD93-18, consists of a truncated caudal vertebral series consisting of two partially preserved distal caudal vertebrae, two chevrons, and a distal unit composed of three fused caudal vertebrae (Fig. 1A–E). The vertebrae can be placed within the distal one third of the tail based on overall morphological similarity (e.g., ratio of centrum length to centrum height) with those known from the near-complete caudal series of FMNH PR 2100 (O’Connor, this volume:table 2, fig. 16). The two preserved chevrons provide no indication of abnormal bone growth; however, the distal portions of these two elements are not preserved.

The first vertebra of the series is a complete centrum and partial neural arch, the latter of which is missing most of the prezygapophyseal and the distal part of the postzygapophyseal processes. Although the overall shape of the centrum is similar to comparable vertebrae from other caudal series of *Majungasaurus*, three subtle features are apparent that presage the pathological condition of succeeding vertebrae. First, there is a slight linear (craniocaudally oriented) exostosis on the right side at mid-centrum height (Fig. 1A). This likely reflects secondary enthesophytic growth that presented subsequent to the primary osteopathy in more distal elements of the series (see below). Second, a small proliferative nodule is present on the ventral midline of the centrum at the edge of the cranioventral chevron facet (Fig. 1A). Finally, a prominent neurovascular sulcus is visible on the left side of the centrum passing from the caudal intervertebral notch to the mid-central ridge (Fig. 1E). Notably, a comparable sulcus is not present on the right side of the centrum, nor have such well defined sulci been observed in vertebrae from numerous other individuals. The cause of this asymmetry remains unclear. The second vertebra of the series, although smaller, is generally similar in overall shape to the first; however, the neural arch is better preserved, missing only the distal portion of the left prezygapophyseal process and the distal portion of the postzygapophyses. Unlike the preceding vertebra, the centrum does not possess any exostotic (or enthesophytic) lesions. However, similar to the preceding vertebra, there is a prominent neurovascular sulcus passing from the caudal intervertebral notch to the mid-central ridge on the left side only. The third, fourth, and fifth vertebrae of the sequence are firmly co-ossified with one another (via both centrum and neural arch components) and dramatically decrease in length such that the ultimate vertebra of the complex is less than one half the length of the first (Fig. 1C). Moreover, the degree of hyperostosis encompassing the final two vertebrae is so extreme as to virtually obscure the normal morphology of the two elements. Importantly, intervertebral disk spaces are obliterated by the osteoproliferative mass (Fig. 1D), thereby ruling out both ankylosing spondylitis and diffuse idiopathic spondylosing hyperostosis (Aufderheide and Rodriguez-Martín, 1998; Mann and Hunt, 2005). Fortunately, patent intervertebral foramina are preserved so as to help demarcate the division between successive elements (Fig. 1A). The neural canal is patent (and presumably the enclosed spinal cord was continuous) throughout the length of the terminal mass and is consistent with the presence of intact spinal nerves and associated vasculature as inferred by patent intervertebral foramina between adjacent vertebrae of the fused complex. Moreover, distinct neurovascular sulci are present and pass

from the intervertebral foramina along the lateral surface of vertebral centra (Fig. 1A).

Although the neural arches are fused among adjacent vertebrae of the terminal mass (Fig. 1B), the most prominent osteopathology is apparent along the ventral and ventrolateral aspect of the last two vertebral centra (Fig. 1C). This region is characterized by extreme hyperostosis associated with numerous cloacae, suggesting chronic suppurative osteomyelitis. The surface texture of the lesion ranges from smooth on the left lateral surface to relatively coarse along the ventral and right lateral surfaces. Numerous smooth walled channels ranging in size from 0.25 to 1.5 mm are present, the majority of which are located along the ventral aspect of the lesion (Fig. 1C). However, a number of cloacae are directed laterally, primarily on the right side of the distal mass. MicroCT imaging of the fused complex indicates the presence of a large (~11 × 9.5 × 8 mm) subspherical cavity located within the ventral half of the distal centrum (Fig. 1D). This cavity is continuous with the extraosseous space via a number of cloacae, thereby supporting the assessment of suppurative osteomyelitis. Finally, the ventral surface of the terminal mass is flattened, a characteristic with at least two possible causes. First, it may merely be primary morphology related to the pathogenic process. In contrast, it may reflect mechanical deformation of the terminal mass resulting from continued contact with the substrate (i.e., tail dragging due to associated neuromuscular dysfunction) subsequent to the initial pathology. The latter scenario is considered much less likely, because the animal probably would not have allowed a presumably painful area to contact the ground continuously.

Based on comparison with the caudal series preserved in FMNH PR 2100, it is predicted that at least 10 additional vertebrae would have been present beyond the distalmost vertebra preserved in FMNH PR 2294. However, the absence of a distinct articular surface on the caudal aspect of the terminal mass of FMNH PR 2294 suggests that the tail terminated at this point. Alternatively (but less likely), the distal portion of the tail remained, but was secured via soft tissue without any osteological contact. Two alternative etiological scenarios are possible for the condition seen in FMNH PR 2294. One possibility is that the end of the tail was lost traumatically, followed by the onset of secondary suppurative osteomyelitis. Alternatively, preexisting osteomyelitis (whether related to trauma, systemic infection, or some other cause) ultimately resulted in the loss of the distal tip of the tail. These alternate scenarios cannot be evaluated based on current data. The presence of cloacae and the complete modification of vertebrae (i.e., the inclusion of both central and neural arch components along with obliteration of the intervertebral disk spaces) rule out other conditions that could contribute to vertebral fusion, such as Paget's disease, ankylosing spondylitis, diffuse idiopathic spondylosing hyperostosis (DISH), and periostosis (Aufderheide and Rodriguez-Martín, 1998; Mann and Hunt, 2005).

Phalangeal Abnormalities

UA 9058 is an isolated left pedal phalanx (III-1 or III-2; Fig. 1I–K) recovered from Locality MAD93-35. The diaphysis of the element is expanded mediolaterally relative to unmodified elements, particularly toward the distal end of the phalanx. The bone texture along the expansion does not differ from that seen in normal phalanges. The profile of the element appears essentially normal in lateral and medial views, and the articular ends of the element show normal morphology. The expanded appearance of the phalanx is suggestive of a healed fracture, but other possibilities such as healed osteomyelitis, a fibro-osseous tumor, bone cyst, metaphyseal dysplasia, or periostitis cannot be excluded.

DISCUSSION AND CONCLUSIONS

The skeletal abnormalities for *Majungasaurus* presented above are restricted to the distal extremities of the skeleton. This is not surprising, as it is expected that the toes and tail would be highly susceptible to injury during an animal's lifetime. Additionally, distal elements were more common in the study sample. Some abnormalities, such as the possible idiopathic ossification of the intervertebral ligaments in FMNH PR 2442, are almost certainly not traumatic or even truly pathological in nature (Hanna, 2002). Others, such as the truncated caudal vertebral series of FMNH PR 2294, are clearly pathological but not unambiguously traumatic. The latter represents the first reported occurrence of such an injury in a theropod dinosaur; among other dinosaurs, a pathologically truncated tail has been reported in only a single hadrosaur specimen (TMP 80.23.2; Tanke and Rothschild, 2002).

Hyperossification of the skeleton in abelisauroids, as exemplified by the generally rugose cranial sculpturing, elongate cervical ribs, hypertrophied epiphyses and expanded tips of the neural spines, is unusual among theropods (O'Connor, this volume; Sampson and Witmer, this volume). However, it is important to emphasize that this is a normal condition among abelisauroids. Similar occurrences in other theropod clades (e.g., tetanurans) may in fact be abnormal, but testing of this inference would require an extensive assessment of inter- and intraclade variability.

Although inferences related to specific events in the life of an animal are typically a major component of studies in dinosaur pathology (e.g., intraspecific 'face-biting' in tyrannosaurs; Tanke and Currie, 1998), the types of abnormalities reported here for *Majungasaurus* are not amenable to precise reconstruction of a traumatic event. Instead, the pathologies and abnormalities documented here are intended for inclusion in broader comparative surveys. Given the ever growing number of well-preserved, associated individuals collected from the Upper Cretaceous Maevarano Formation, *Majungasaurus* will continue to provide important information related to the assessment of skeletal pathology in dinosaurs, rivaling those taxa (e.g., *Allosaurus*) historically used in studies of pathology and general theropod bone biology.

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